

CHROMOSOME CONSTITUTION IN CERTAIN MONOCOTYLEDONS

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With nine text figures

MCKELVEY AND SAX (1933) have called attention to the existence of taxonomic and cytological similarities between certain genera in the Liliaceae and Amaryllidaceae. The similarity is rather striking with regard to chromosome constitution. *Yucca*, *Hesperoyucca*, *Cleistoyucca*, *Hesperaloë*, and *Samuela*, in the Liliaceae, all have 5 long and 25 short chromosomes. *Agave* in the Amaryllidaceae has exactly the same chromosome constitution. These observations when considered in conjunction with taxonomic resemblances, seem to indicate that the genera mentioned above are more closely related than is shown by their separation into distinct families. With the object of discovering whether this pronounced heteromorphism (5 long and 25 short chromosomes) is of general occurrence throughout the monocotyledons, a number of species have been examined.

After a casual survey, the species enumerated below were selected for further study as being the most interesting from the point of view of the problem under investigation.

1. *Polygonatum tuberosum* L. Amaryllidaceae
2. *Fourcroya gigantea* Vent. Amaryllidaceae
3. *Fourcroya Selloa* C. Koch Amaryllidaceae
4. *Fourcroya Bedinghausii* C. Koch Amaryllidaceae
5. *Doryanthes Palmeri* W. Hill Amaryllidaceae
6. *Hosta coerulea* (Andrews) Tratt. Liliaceae
7. *Dasylyris longissimum* Lem. Liliaceae
8. *Nolina recurvata* Hemsl. Liliaceae
9. *Butomus umbellatus* L. Butomaceae

The chromosome counts were secured from root-tip material, prepared by the smear-maceration method and stained with aceto-carmin (Whitaker, 1934). In the case of *Hosta* and *Polygonatum*, the root-tip material has been augmented by counts from pollen mother cells.

Chromosome counts during meiosis indicate that *Polygonatum tuberosum* has 30 chromosomes. The chromosome constitution in this species is identical with that of the *Yucca-Agave* group. The shape and size of

the 5 long chromosomes are comparable with figures from similar stages in either *Yucca* or *Agave* (Fig. 1).

In *Fourcroya gigantea* the somatic chromosome number appears to be 60. The chromosome complement of this species consists of 10 distinctly long chromosomes and 50 short ones (Fig. 2). Counts from root-tip cells of *F. Bedinghausii* and *F. Selloa* show that these two species also have 60 somatic chromosomes. The morphology of the chromosome complement in the case of the latter two species is the same as that of *F. gigantea*.



FIGURE 1. *POLYANTHES TUBEROSA*. 30 chromosomes at metaphase. About $\times 2100$. — FIGURE 2. *FOURCROYA GIGANTEA*. 60 chromosomes at metaphase. About $\times 2100$.

Doryanthes is the sole representative of the sub-family Agavoideae not indigenous to the desert areas of North America. The three species of this genus are all natives of Australia. *Doryanthes Palmeri*, the species from which the material was secured, has 36 somatic chromosomes (Fig. 3). On morphological grounds the chromosome complement of this species is not at all comparable with that of the North American species of the Agavoideae (compare Fig. 2 with Fig. 3). The 5 long pairs of chromosomes which are one of the conspicuous features of the chromosome set-up in *Agave*, *Yucca*, *Fourcroya*, etc. are absent in *Doryanthes Palmeri*. Long and short chromosomes are present, but there is not the same degree of difference which exists between the long and short chromosomes of the *Yucca-Agave* group. Thus there are two categories of evidence, cytological and distributional, which are opposed to the placing of *Doryanthes* in the sub-family Agavoideae.

Hosta coerulea has 30 meiotic chromosomes (Fig. 4). The chromosome constitution in this species appears to be similar to that of the *Yucca-Agave* group. There exists the possibility that one of the long chromosomes may not equal the size of the four remaining long ones. If this difference exists, it is slight, and with this exception, it is clearly apparent that the chromosome morphology of this species is

fundamentally the same as that found in *Yucca*, *Agave*, *Fourcroya*, etc. Miyake (1906) has figured the chromosomes of *Hosta Sieboldiana*. His figures show the 5 long chromosomes quite plainly, but the total number seems to be somewhat less than the 30 pairs found in *H. coerulea*. It is interesting to note that the 5 long chromosomes were also found in *H. Sieboldiana*.

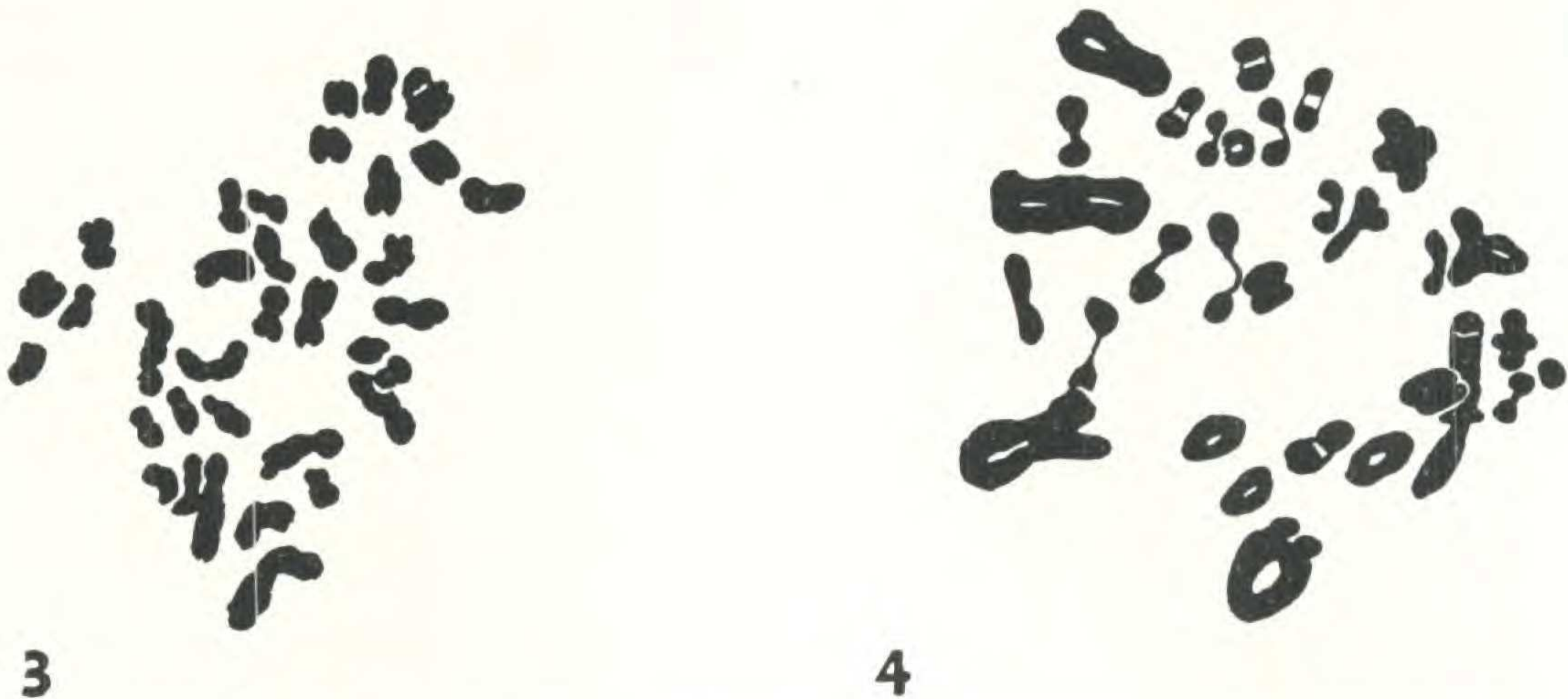


FIGURE 3. *DORYANTHES PALMERI*. 36 chromosomes at metaphase. About $\times 2100$. — FIGURE 4. *HOSTA COERULEA*. 30 chromosomes at diakinesis. About $\times 2500$.

Dasyilirion, *Nolina*, and *Dracaena* have been examined with the purpose of discovering a possible connecting link between these genera and the *Yucca-Agave* group. According to Johnston (quoted in McKelvey and Sax, 1933), if an affinity between the *Yuccas* in the Liliaceae and the *Agaves* in the Amaryllidaceae is to be established, it is most likely to be traced through the genera mentioned above. *Dasyilirion* and *Nolina*, have distributions which closely parallel that of the *Yucca-Agave* group. Cytologically *Nolina* has nothing to contribute to the problem. *Nolina recurvata* has 36 pairs of chromosomes (Fig. 5) which are of approximately equal length. The attachment constrictions are median or sub-median in most cases.

Dasyilirion longissimum seems to have 38 chromosomes, three pairs of which are very nearly twice the length of the shorter chromosomes (Fig. 6). The size difference between the long and short chromosomes of this species are not nearly as striking as the differences existing in the chromosome complement of the members of the *Yucca-Agave* group.

Dracaena arborea has about 38 chromosomes, according to McKelvey and Sax (1933). The writer has examined another species of *Dracaena* (*D. fragrans* Ker-Gawl.). This species also seems to have about 38

chromosomes, all of which are very small and very nearly of equal length.

So far as the cytological observations already completed are concerned, *Nolina*, *Dracaena*, and *Dasyilirion* obviously do not point the way to further progress with the problem. *Nolina* and *Dracaena*, by reason of the morphology of their chromosome complements, can be eliminated from further consideration. *Dasyilirion* has possibilities, but on the basis of its chromosome complement alone, there are not sufficient grounds for thinking of it as closely allied to the *Yucca-Agave* group.

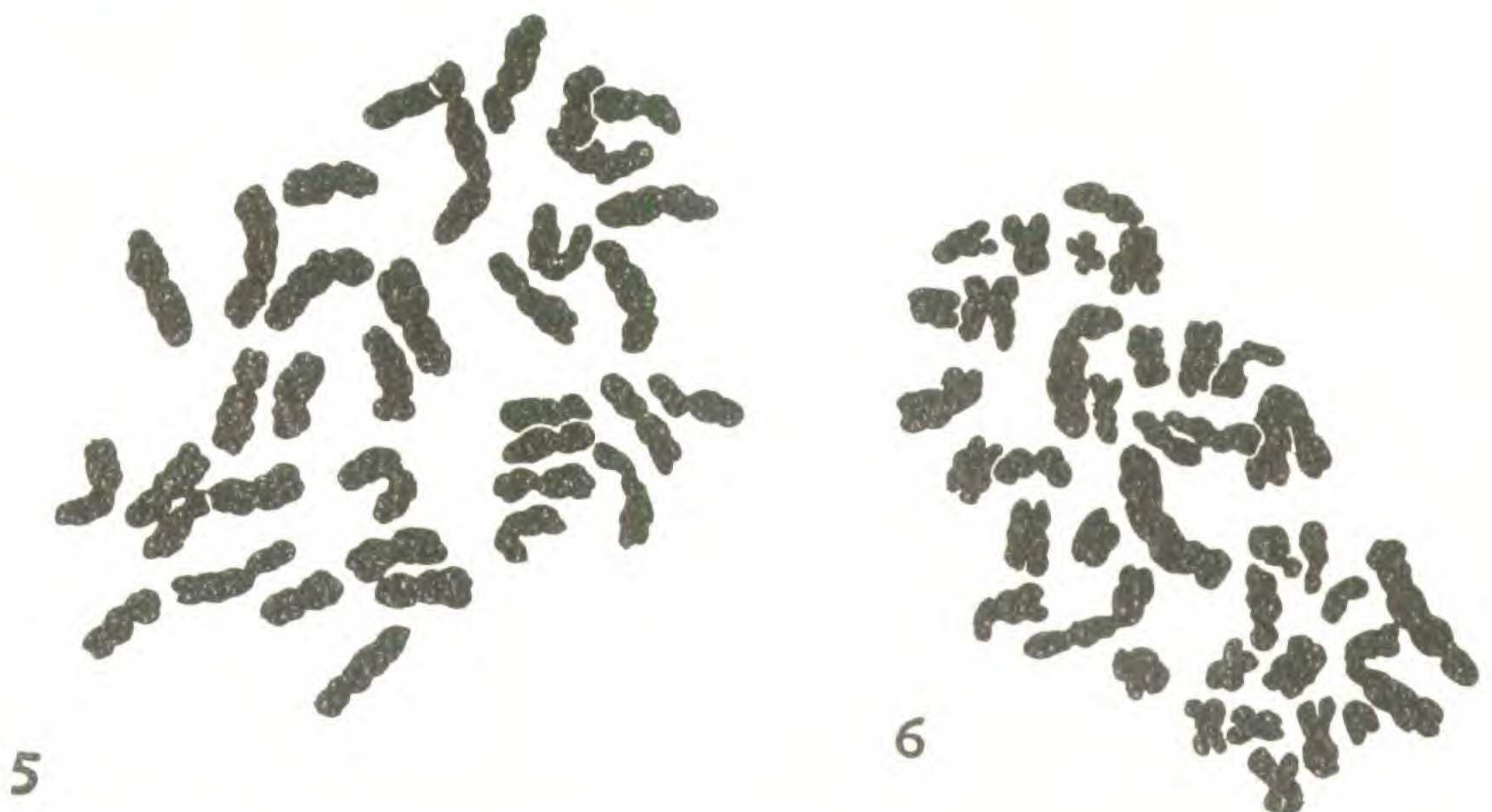


FIGURE 5. *NOLINA RECURVATA*. 36 chromosomes at metaphase. About $\times 2500$.—FIGURE 6. *DASYILIRION LONGISSIMUM*. 38 chromosomes at metaphase. About $\times 2500$.

*Butomus umbellatus*¹ has 26 somatic chromosomes (Fig. 7). Early studies on embryo sac development, where chromosome number was reported incidentally, have led to some confusion. Holmgren (1913) has stated that the reduced number in this species is 11-12. Liehr (1916) has placed the reduced number at 8. Terby (1922), who has evidently made a very careful study of the somatic chromosomes of this species, finds 40 chromosomes. Apparently the plant or plants from which she secured her material must have been triploid in origin. In Fig. 7, where the 26 somatic chromosomes of *Butomus umbellatus* are shown at metaphase, four pairs are noticeably longer than the remainder. It is this situation which suggests that Terby's material may have been of

¹The writer is indebted to Professor C. L. Huskins, McGill University, Montreal, Canada, for the material of *Butomus umbellatus*.

triploid nature because if another genom of 13 chromosomes were added to the diploid complement of Fig. 7, there would be twelve long chromosomes, and that is exactly what happens, as the reproduction of Terby's figure shows (Fig. 8).

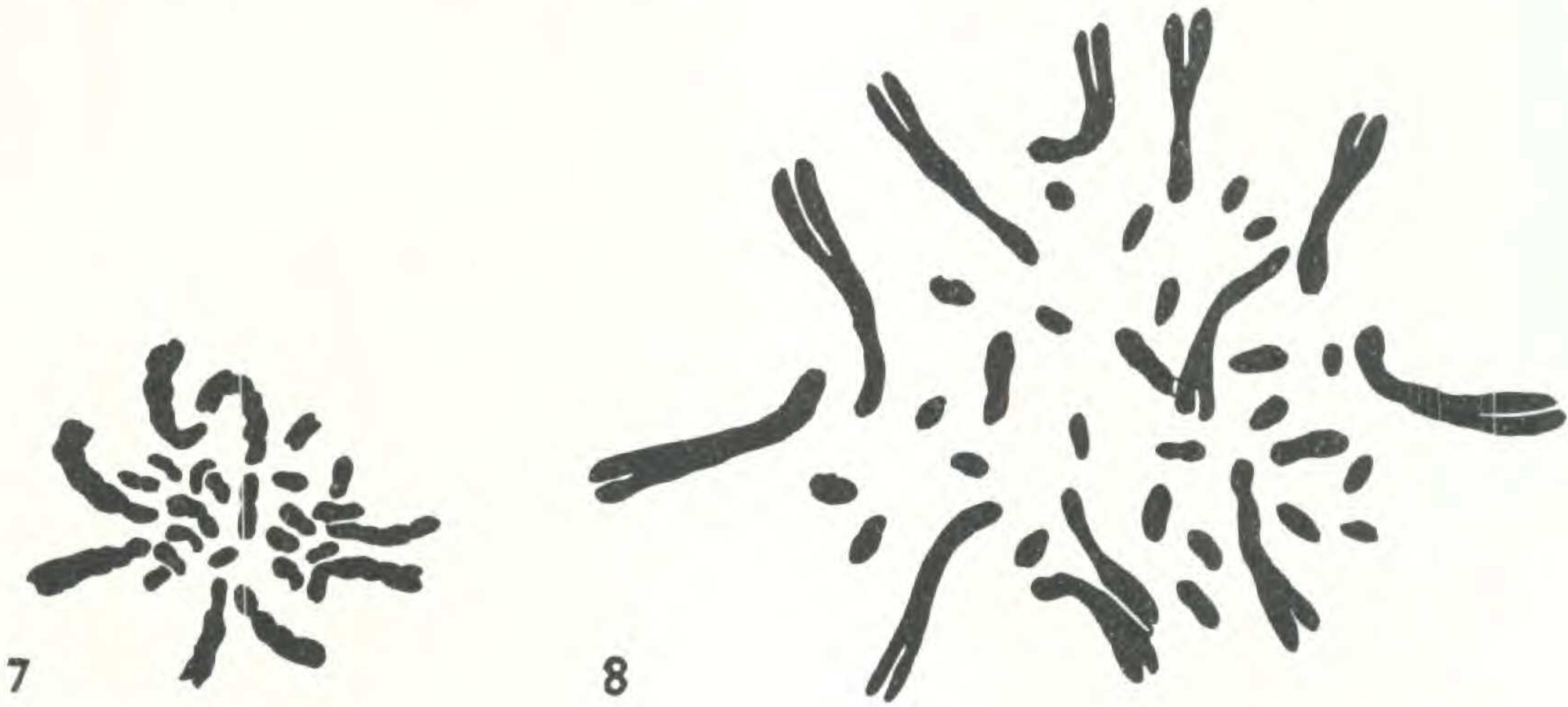


FIGURE 7. *BUTOMUS UMBELLATUS*. 26 chromosomes at metaphase. About $\times 2500$. — FIGURE 8. *BUTOMUS UMBELLATUS* (probable triploid, after Terby).

The purpose of studying the chromosome complement of this species was to indicate that the size differences among the chromosomes are of the same general order as those found in *Yucca*, *Fourcroya*, *Agave*, etc. That this is actually the case is fully substantiated by a comparison of the chromosomes of *B. umbellatus* (Fig. 7) with those of members of the *Yucca-Agave* group, *Fourcroya* for instance (Fig. 2).

DISCUSSION

Heitz (1926) mentioned the correlation existing between taxonomy and chromosome constitution in the Agavoideae. His observations on *Fourcroya*, and those of Müller (1912) on *Beschorneria* and *Agave*, led to this conclusion. He states that not only do these genera belong to the same sub-family (Agavoideae), but they are also characterized by the same sort of chromosome constitution.

McKelvey and Sax (1933), as stated previously, have pointed out the similarities with respect to chromosome constitution between the *Yuccae* and the Agavoideae. The chromosome set-up of representative species of these two groups is strikingly similar, and in all visible respects, identical. These investigators have stated that it is unlikely that this is due to chance but must mean that these two groups are more closely akin to each other than is indicated by the prevailing system of classification which separates them into different families.

It is clear, from this brief review of previous work, that the point to be emphasized is that a chromosome set consisting of 10 long and 50 short chromosomes is sufficiently uncommon in the plant kingdom to lead one to suspect that species having this unique chromosome constitution are of common ancestry and closely related.

The present observations on *Polyanthes* and *Fourcroya* added to those of previous investigators, give a fairly complete story in regard to chromosome constitution in the Agavoideae. Pax and Hoffmann (1930) have listed seven genera belonging to this sub-family. Disregarding *Doryanthes*, which does not seem to fit into this group, four of the remaining genera have been examined, and all have exactly the same chromosome set-up. There are some possible exceptions. Heitz (1926) has reported *Fourcroya Lindenii* as having 10-12 long and 30-39 short chromosomes, and *F. altissima* with 10 long and 40 short chromosomes. It is likely that this may be an error, for the reason that the three other species of *Fourcroya* examined all have the usual complement of 10 long and 50 short chromosomes. These observations very definitely indicate a close cytological relationship between the members of this sub-family. It is reasonable to suppose that the members of the Agavoideae are taxonomically closely allied to the Yuccae. Johnston (quoted in McKelvey and Sax, 1933) has listed a number of similarities between these two groups.

To state the essential facts in a more concise form, we have five genera in the Liliaceae (*Hesperaloë*, *Hesperoyucca*, *Cleistoyucca*, *Yucca*, *Samuela*) and four genera in the Amaryllidaceae (**Fourcroya*, *Agave*, *Beschorneria*, *Polyanthes*), which, on distributional, taxonomic, and cytological grounds, are closely akin to each other. These facts should be given serious consideration in any taxonomic revision of these two families where an attempt is made to arrange the genera in a phylogenetic series.

In regard to *Hosta*, the situation is difficult to interpret. There can be little doubt that it is similar in chromosome constitution to the *Yucca-Agave* group. A careful study of a number of slides has not revealed a single consistent difference by which one would be able to distinguish the chromosome complement of the two species under discussion. *Hosta*, as now constituted, is placed in the sub-family Asphodeloideae, rather widely separated from *Yucca*, which has been placed in the Dracaenoideae (Krause, 1930). Superficially, the resemblance between *Hosta* and members of the *Yucca-Agave* group are

**Prochnyanthes* and *Pseudobravoia* are genera which fit into this group on distributional and taxonomic grounds. Species of these genera were not available for cytological studies and consequently had to be omitted.

slight enough to be almost negligible. If we retain the original supposition that the possession of an identical chromosome complement is an indication of a comparatively close relationship, it must mean that it is possible to obtain a far-reaching differentiation of specific characters without a drastic change in the morphology of the chromosome complement. It is probable that chromosome constitution may behave in a manner comparable to many morphological characters, that is to say, a certain character may flow along with the main body of evidence and then suddenly diverge to a point where it is no longer of significance. Therefore, chromosome constitution as a criterion of phylogenetic relationship should only be judged in so far as it fits in with other lines of evidence.

There is some cytological evidence suggesting that the peculiar heteromorphic chromosome set-up found in the *Yucca-Agave* group may indicate a fundamental relationship which can be traced through a number of families in the monocotyledons.

The evidence for the existence of this relationship is derived from both taxonomy and cytology, and seem to point to the following conclusions:

1. There is a group of families in the Helobiae, which represent primitive generalized types.

2. It appears as if the specialized chromosome set-up of the *Yucca-Agave* group may have had its origin among the families of this order.

In the classification of Wettstein (1924), the Helobiae are considered the most primitive monocotyledenous group. In this order occur among others, such presumably primitive families as Butomaceae, Najadaceae, Hydrocharitaceae, Triuridaceae, etc. If the chromosome complement of species representing the four families mentioned above is analyzed, some rather striking similarities are apparent. There are either four or five pairs of long chromosomes associated with a varying number of short ones, no single one of which is equal to one half the length of the longer chromosomes. The attachment constriction is either median or sub-terminal in the long chromosomes and usually terminal in the short chromosomes.

In Fig. 9, the five longest chromosomes from representative species of the four families listed above have been drawn diagrammatically. The measurements have been made from metaphase plates during mitosis. The drawings have been reduced to approximately the same scale. These diagrams seem to verify the assertion that there is some measure of similarity between the five longer elements in the chromosome complement of some of the species of these four families (Butomaceae, Hydrocharitaceae, Najadaceae, Triuridaceae).

The point I wish to make, in presenting this evidence, is that the five longer elements in the chromosome complement of these four species, show some resemblance to each other; and, furthermore, they are of the same general nature as that of the five longer elements in the chromosome complement of members of the *Yucca-Agave* group. This may well be a superficial resemblance of no significance whatever, but the taxonomic and cytological evidence combine to give it a certain weight worthy of more extended investigation.

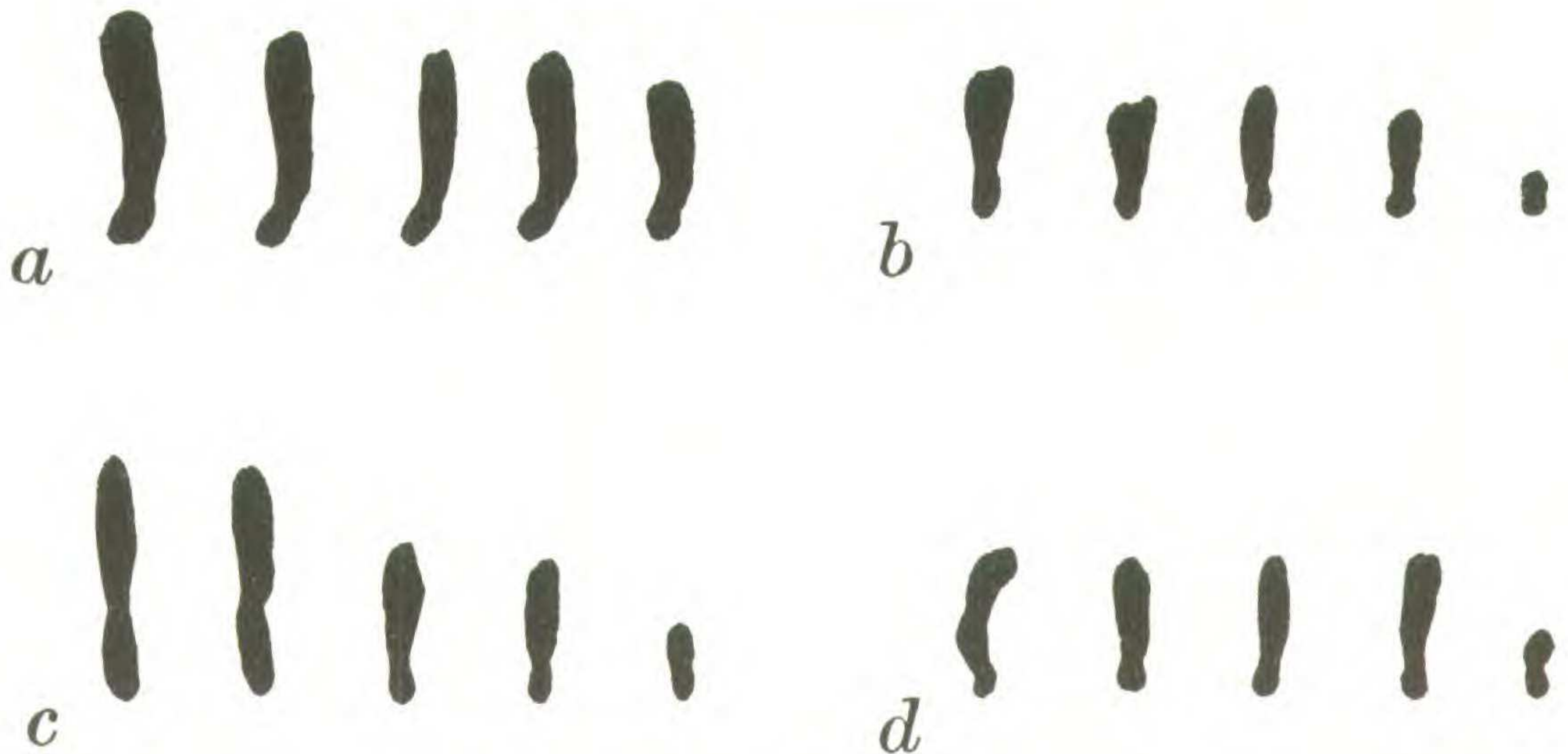


FIGURE 9. a. *NAJAS MARINA* L. (after Winge). — b. *VALLISNERIA SPIRALIS* L. (after Winge). — c. *SCIAPHLIA JAPONICA* Mak. (after Ohga and Sinoto). — d. *BUTOMUS UMBELLATUS* L.

As previously stated, Wettstein (1924) from taxonomic considerations has shown that the Helobiae are the most simple and probably the most primitive of the monocotyledons. There are very good reasons for thinking that the Liliiflorae have been derived from this group. (Janchen, 1932). It is interesting to find that the very specialized chromosome constitution of 5 long and 25 short chromosomes, characteristic of the *Yucca-Agave* group, may well have had its origin in the Helobiae.

SUMMARY

Combining the results of previous workers with those of the present investigation, it has been possible to show that five genera in the Liliaceae (*Yucca*, *Hesperoyucca*, *Hesperaloë*, *Cleistoyucca*, *Samuela*) and four genera in the Amaryllidaceae (*Agave*, *Fourcroya*, *Polyanthes*, *Beschorneria*) form a distinct unit and as such should be united in any future revision of these two families. The evidence for this unity is based on geographic distribution, taxonomic and cytological similarities.

There is some evidence indicating that the heteromorphic chromosome set-up found in the *Yucca-Agave* group may be of general occurrence in the monocotyledons. *Hosta* in the Liliaceae has a chromosome complement identical with this group. Several species in the Helobiae have been shown to have a chromosome set-up from which that found in the *Yucca-Agave* group may have been derived.

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LITERATURE CITED

- HEITZ, E. (1926). Der Nachweis der Chromosomen. (Zeitschr. f. Bot. **18**:625-681.)
- HOLMGREN, J. (1913). Zur Entwicklungsgeschichte von *Butomus umbellatus* L. (Svensk. Bot. Tids. **7**:58-77.)
- JANCHEN, E. (1932). Entwurf eines Stammbaumes der Blütenpflanzen nach Richard Wettstein. (Oesterr. Bot. Zeitschr. **81**:161-165.)
- KRAUSE, K. (1930). Liliaceae. (Engler & Prantl, Nat. Pflanzenfam. ed. 2, **15a**:227-390.)
- LIEHR, O. (1916). Ist die angenommene Verwandtschaft der Helobiae und Polycarpicae auch in ihrer Cytologie zu erkennen? (Cohns Beitr. Biol. Pflanz. **13**:135-220.)
- McKELVEY, S. D. and SAX, K. (1933). Taxonomic and cytological relationships of *Yucca* and *Agave*. (Jour. Arnold Arb. **14**:76-80.)
- MIYAKE, K. (1906). Histologische Beiträge zur Vererbungsfrage. III. Ueber Reduktionsteilung in den Pollenmutterzellen einiger Monokotylen. (Jahrb. Wiss. Bot. **42**:83-120.)
- MÜLLER, C. (1912). Kernstudien an Pflanzen. I, II. (Arch. Zellforsch. **8**:1-51.)
- OHGA, I., and SINOTO, Y. (1924). Cytological studies on *Sciaphila japonica* Mak. I. On chromosome. (Tokyo Bot. Mag. **38**:202-207.)
- PAX, F. and HOFFMANN, K. (1930). Amaryllidaceae. (Engler & Prantl, Nat. Pflanzenfam. ed. 2, **15a**:391-430.)
- TERBY, J. (1922). La constance du nombre des chromosomes et de leurs dimensions dans le *Butomus umbellatus*. (La Cellule, **32**:197-226.)
- WHITAKER, T. W. (1934). An improved technique for the examination of chromosomes in root-tip smears. (Stain Technology, *in press*.)
- WINGE, O. (1927). Chromosome behavior in male and female individuals of *Vallisneria spiralis* and *Najas marina*. (Jour. Genetics, **18**:99-107.)

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